

Relative Suitability of Virginia Pine and Loblolly Pine as Host Species for *Dendroctonus frontalis* (Coleoptera: Scolytidae)

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ABSTRACT *Dendroctonus frontalis* Zimmerman is a major disturbance agent in American pine forests, but attack preferences for various host species, and their relative suitability for reproduction, are poorly known. We studied patterns of beetle attack and reproduction during an infestation of stands containing Virginia pine and loblolly pine. Nearly all Virginia pine were attacked and killed, whereas a third of the loblolly pine escaped attack. Among attacked trees, the density of landings and attacks on Virginia pine was 56–106% higher than on loblolly pine at one site, whereas it was similar between species at another site. Paradoxically, *D. frontalis* preferred the host that was least suitable for reproduction: mean \pm SE = 0.89 ± 0.33 versus 4.65 ± 1.40 progeny/attack in Virginia pine versus loblolly pine. Poor reproduction in Virginia pine was attributable to increased adult mortality, decreased oviposition, and decreased larval survival. Phloem thickness and nitrogen content were similar between the two pine species. Loblolly pine was significantly more suitable for the growth of *Ophiostoma minus*, a fungal associate of *D. frontalis*. Resin flow was lower in Virginia pine than in loblolly pine, although oleoresin chemistry may partly explain poor reproduction in Virginia pine. A simulation model predicted that beetle infestations will tend to collapse within stands dominated by Virginia pine, and that increasing availability of loblolly pine will promote infestation growth. Because of beetle preferences, forests that contain even modest proportions of Virginia pine relative to loblolly pine may be less likely to sustain beetle infestations. Management of species composition may provide a means for mitigating the undesirable impacts of this herbivore in pine forests.

KEY WORDS forest management, host selection, secondary attraction, oleoresin, population dynamics

SOME FOREST INSECTS, including most of the economically important herbivores, exhibit dramatic fluctuations in abundance. Understanding the causes of these fluctuations is of basic interest in population ecology (Turchin and Taylor 1992, Kendall et al. 1999) and has applied value to forest managers (Ayres and Lombardero 2000). *Dendroctonus frontalis* Zimmerman (Coleoptera: Scolytidae), the southern pine beetle, undergoes 8–12-yr population cycles, during which the number of infestations in a region can vary dramatically (e.g., from 0 to 7500 discrete infested stands in east Texas; Turchin et al. 1991). Tens to thousands of healthy pine trees are killed within one year by a single infestation (Billings 1994), causing direct economic losses of up to \$121 million a year to the forest products industry (Price et al. 1997).

Dendroctonus frontalis can attack and kill at least 18 different species of *Pinus* (Payne 1980), six of which

are common in the southeastern United States: *P. taeda* L., *P. virginiana* Mill., *P. echinata* Mill., *P. elliotii* Engelm. variety *elliottii*, *P. palustris* Mill., and *P. strobus* L. However, literature on the relative suitability of host species is largely qualitative (Dixon and Osgood 1961, but see Cook and Hain 1985), which makes it difficult to evaluate the effects of host species on beetle population dynamics. The quantitative effects of host species on beetle reproduction are relevant to whether management of pine species composition could potentially mitigate undesirable impacts of this herbivore on forest ecosystems. In this study, we tested for effects of host species on beetle reproductive success within mixed species stands. We also tested whether beetles attacked one or the other species preferentially, which could affect the demographic consequences of differences in host suitability.

In general, colonization of host plants by insect herbivores involves habitat finding, host finding, host recognition, host acceptance, and host suitability (Kogan 1994). In the case of epidemic populations of *D. frontalis*, several thousand beetles participate in the

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rapid (5–15-d) mass attack of individual trees within a local infestation (Fargo et al. 1978, Bunt et al. 1980). Host finding, host recognition, and host acceptance by *D. frontalis* involve olfaction, vision, mechanoreception, and contact chemoreception, probably to varying degrees depending on the stage of attack (i.e., initial colonization versus aggregation phase versus termination) (Kinzer et al. 1969, Raffa and Berryman 1982, Strom et al. 1999). The plume of host volatiles (e.g., α -pinene) and aggregation pheromone (frontalin) that flows from a tree under early attack is a powerful attractant for more beetles (Payne 1986). Later, the production of an anti-aggregation pheromone (verbenone) dramatically decreases host attraction (Salom et al. 1992). Once an adult beetle penetrates the phloem during attack, it often encounters oleoresin, a mix of monoterpenes and resin acids that flows into wounds from sites of synthesis and storage in the resin duct system of the xylem (Lombardero et al. 2000). Oleoresin serves as a physical barrier to the excavation of oviposition galleries (Reeve et al. 1995), inhibits the release of aggregation pheromones (Raffa and Berryman 1983), and can be toxic to the beetle (Coyne and Lott 1976). In loblolly pine, depletion of constitutive oleoresin, as during beetle attack, induces rapid biosynthesis of additional (inducible) resin, which may further impede beetle colonization, especially when attack rates are low (Ruel et al. 1998, Lombardero et al. 2000). Host suitability for *D. frontalis* may be influenced by the efficacy of this resin defense system (Hodges et al. 1977, 1979). In general, the greater the resin flow of a tree, the lower the per capita oviposition success of the beetles (eggs/female; Reeve et al. 1995).

Dendroctonus frontalis reproduction is also a function of the suitability of the phloem to the beetle and its three primary fungal associates (Cook and Hain 1987, 1988). *Dendroctonus frontalis* larvae depend on two mutualistic fungi, *Ceratocystiopsis ranaculosus* Perry and Bridges and *Entomocorticium* sp. A., for nutrition and proper development (Barras 1973, Goldammer et al. 1991, Coppedge et al. 1995). These fungi enter the host from the mycangium of adult female *D. frontalis* (Barras and Perry 1972) and concentrate nitrogen needed by larvae (Ayres et al. 2000). Growth of these mutualistic fungi may be influenced by phloem chemistry (Bridges 1987) and competitive interactions with other fungi. In particular, larvae seldom survive in the presence of the bluestain fungus, *Ophiostoma minus* (Hedgecock) Hunt (Barras 1970, Lombardero et al. 2003), which tends to outcompete mycangial fungi (Klepzig and Wilkens 1997), and provides inadequate dietary protein for larvae (Ayres et al. 2000).

Ophiostoma minus is transported between trees by two species of mites, *Tarsonemus krantzi* Smiley and Moser and *T. ips* Lindquist, that are phoretic on *D. frontalis* (Bridges and Moser 1983, Smiley and Moser 1974). Within trees, *O. minus* propagules are dispersed by mites within the phloem surrounding beetle galleries (Lombardero et al. 2003), and within the resin duct system by the resin itself (Whitney and Blauel

1972). The mites, in turn, feed on *O. minus* (Moser and Bridges 1986). Thus, *Tarsonemus* spp., by increasing the abundance of *O. minus*, may exert indirect negative effects on *D. frontalis* (Klepzig et al. 2001, Lombardero et al. 2003).

There may be ramifications of forest composition for beetle population dynamics if host species differ in (1) their resin defense systems, (2) their suitability for fungi that are mutualistic versus antagonistic, or (3) their density of mites.

Materials and Methods

Studies were conducted within mixed species stands of Virginia pine, *P. virginiana*, and loblolly pine, *P. taeda*, in the Bankhead National Forest, AL (35° N, 87° W) during a natural outbreak of *D. frontalis* that involved ≈ 1000 local infestations of 0.1–100 ha each during 1998–2001. Most measurements were collected within three 1-ha study sites separated by 100–500 m within a tract of continuous forest. Two years later, we measured resin flow in one additional study site that was 25 km away (because most pines had been killed in the vicinity of the original plots). Trees of both species averaged 20–30 cm in diameter, 18–22 m tall, and 25–30 yr old. The relative abundance of loblolly and Virginia pine was similar within sites (1:1–6:4). Hardwoods, which accounted for 20–40% basal area, included *Quercus* spp., *Acer rubrum*, *Liquidambar styraciflua*, *Magnolia macrophylla*, *Liriodendron tulipifera*, *Cornus* spp., and *Sassafras albidum*.

Resin Defenses in Experimentally Wounded Trees. We compared the amount of resin that flowed from standardized wounds applied to both Virginia pine and loblolly pine: $n = 15$ intermixed, uninfested trees of each species (site 1). Methods followed Ruel et al. (1998) and Lombardero et al. (2000). On 29 April 1999, at 0900 hours, two disks (125 mm²) of bark and phloem were removed from each tree and the resin that flowed from exposed xylem was collected over 3 h. At 1230 hours, two horizontal strips of bark were removed from one side of each tree (3 cm \times one-half-tree-circumference; at 22 cm above and below the sampling points). At 1330 hours, both wounds were enlarged by removing another, horizontal strip of bark (1.5 cm \times one-half-tree-circumference). This wounding regime allowed copious resin flow and depleted the xylem resin ducts on that side of the tree. At 0900 hours on 30 April 1999, resin flow from 125 mm² wounds was sampled as before from both sides of the tree (depleted and control). At 1230 hours, the depletion wounds were enlarged by removing two more horizontal strips of bark (1.5 cm \times one-half-circumference). Seven days later (6 May), resin flow was sampled as before, from new 125-mm² wounds on both sides of each tree. This protocol provided measures of constitutive resin flow, extent of depletion from standardized wounds, and inducible response of the resin duct system to resin depletion (Lombardero et al. 2000). Resin flow data (g/wound) were square-root transformed and analyzed with an analysis of variance (ANOVA) model that included species, day,

and resin depletion treatment as fixed effects, and tree nested within species as a random effect.

We performed an additional study to test for differences between pine species in how long oleoresin flows from a wound. On 31 August 2001, we chose 10–12 trees of both species that were interspersed within a different 1-ha site (site 4, 25 km east of sites 1–3). We applied two standardized wounds to each tree as before (125 mm² diameter) and measured the resin flow from each wound after 3 h, 24 h, and 72 h.

Beetle Attack Preferences and Resin Flow During Attacks. In mid July 1999, we chose 15 similar uninfested trees of both pine species within a 1-ha site (site 2) that was just in front of an advancing infestation of *D. frontalis*. Individuals of both pine species were thoroughly intermixed within the plot. Pre-attack resin flow was measured every other day from 20 to 28 July 1999 (two 125-mm² wounds per tree per day, as described above). On 28 July, to increase the probability that our study trees would be attacked by the advancing infestation, we baited 11–12 trees of each species at 3 m height with frontalin and turpentine (following the methods of Billings 1988). Baits were randomly placed with respect to cardinal directions. Four Virginia pine and three loblolly pine were left unbaited as controls. All 30 study trees, and many other trees in the same stand, came under attack within the next 10 d. We continued measuring resin flow every other day through 26 August.

During attacks, densities of landing beetles were quantified using pairs of sticky traps (30 × 15-cm plywood boards) covered with an adhesive (Stikem Special, Michel and Pelton Company, Emeryville, CA) and treated with a pyrethrin-based insecticide. One pair of traps was randomly oriented with respect to cardinal direction on opposite sides of each tree at 2.5 m height. From 28 July to 26 August 1999, these traps were scored every other day for captures of *D. frontalis* and *Thanasimus dubius* (Coleoptera: Cleridae; the dominant predator of *D. frontalis*; Berisford 1980, Turchin et al. 1999). These data permitted a comparison of beetle preferences, as expressed by landing rates, for the two pine species during the stage of secondary attraction following initial attack (based on a random sample of trees of each species that came under attack in the same site at the same time).

During the same period, we counted pitch tubes (each representing one attack by a pair of beetles), in each of two, 66 × 7-cm plots/tree that were lightly shaved of the outer bark to ensure that no attacks were concealed from view. Each pair of plots was located at 2.5 m height, on opposite sides of the trunk, such that each plot was between the tree's two sticky traps. We also counted pitch tubes over the entire lower bole from 2 to 5 m in height, including the shaved and unshaved areas. Analyses revealed that attacks within plots were linearly correlated with total attacks on the bole ($r^2 = 0.67$ and 0.37 for Virginia pine and loblolly pine, respectively). Thus, in later analyses, we used attack densities from the entire lower bole because they comprised a larger sample of attack events over the whole tree.

For each tree, total landings/m² and attacks/m² were regressed separately against days since the first attack. Examination of scatter plots indicated that the relationship was approximately linear on each tree. The slope of each line represented the daily landing rate or attack rate for the tree, and the x-intercept represented the date of attack initiation. The ratio of attacks/landing gave an independent measure for each tree of the probability that a landing beetle entered the tree. Attack initiation dates, landing densities, attack densities, and attacks/landing were compared between tree species with a *t*-test. Attack densities and attacks/landing were log transformed to normalize data and correct for heteroscedasticity. These and other statistical analyses were performed using JMP software (SAS Institute 1999).

We summarized the dynamics of each tree's oleoresin system during attack by calculating the slope of resin flow regressed against day of attack (slope = Δ resin/d). A positive slope indicated increasing resin flow during the course of attack and a negative slope indicated decreasing resin flow. We tested for species differences in oleoresin dynamics (Δ resin/d) during attack with a *t*-test comparing pine species, and a general linear model that included pine species, final attack density, and species × attack density.

On 22 June 2000, we classified each of the 105 loblolly pine and Virginia pine in site 2 as having been attacked or not attacked during the previous year, and scored each tree for survival. The likelihood of *D. frontalis* attack and survival was compared between tree species with a *G* test. The comparison of attack probabilities complimented measurements of landing rates during attack (secondary attraction) by testing for host preferences in terms of primary attraction.

Colonization Success of *D. frontalis*, *O. minus*, and *Tarsonemus*. On 20–28 August 1999, we collected two 9 × 27-cm bark samples from 10 Virginia pine and 8 loblolly pine. All samples were taken at a height of 2 m from infested trees that contained late-instar larvae or pupae. These trees were within a 1-ha area (site 3) ≈100 m distant from site 2. Trees on site three were infested by the same local population of beetles as those on site 2, but differed in having been attacked 2–3 wk earlier. Site 3 further differed in that the two pine species tended to be segregated in opposite corners of the 1-ha plot (rather than interspersed as in the other study sites). For each bark sample, we counted the corpses of attacking adults that did not reemerge, and measured (1) the length of oviposition gallery, (2) the number of eclosed larvae (indicated by the initiation of feeding chambers), (3) the number of pupation chambers (indicating larvae that would have survived to become adults), (4) the number of entry holes (each indicating one pair of attacking adults), (5) percent area covered with *O. minus* hyphae and perithecia (bluestain), and (6) density of *Tarsonemus* mites. *Tarsonemus* mites (all life stages) were counted in five randomly placed 1-cm² plots per bark sample. If the majority of the bark sample was covered with bluestain, then three of the 1-cm² plots were in areas with, and two were in areas without, bluestain. Oth-

erwise, two of the 1-cm² plots were in areas with, and three were in areas without, bluestain. The total number of mites/250 cm² was estimated by multiplying the average number of mites found in each type of subplot (*O. minus* or non-*O. minus*) by the total area of that type within the larger 250-cm² plot, and then adding the results of the two types of subplots. For each bark sample, we also calculated larval survival as pupae/hatched larvae; hatched larvae/dm oviposition gallery; and the probability that attacking adults re-emerged to attack another tree as $1 - \text{dead adults} / (2 \cdot \text{attack entries})$. Those adults consumed by predators would not be accounted for by these reemergence estimates, but *T. dubius* landing densities were similar between tree species, so predation rates within the phloem were probably also similar. Data were analyzed with an ANOVA model that included species as a fixed effect, and tree nested within species as a random effect. Hatched larvae, oviposition gallery length, and hatched larvae/dm oviposition gallery were square-root transformed, and mite abundance was log transformed, to correct for heteroscedasticity.

To further investigate the colonization success of fungal associates of *D. frontalis* in each tree species, we compared the relative abundance of fungal propagules carried by flying *D. frontalis* adults (captured in Lindgren traps), with *D. frontalis* adults excavated on the same day from fresh attacks (<24 h old, indicated by incompletely crystallized pitch tubes) on Virginia pine and loblolly pine adjacent to the Lindgren traps. Adults were placed individually in a solution of the surfactant Niaproof (Sigma Aldrich, St. Louis, MO). On 20 October 1999, the Niaproof + beetle solutions were plated on malt agar and incubated at 25°C for 14 d. All resulting fungal colonies on each plate were counted. We measured 8–10 beetles from each of the three treatments. Colony numbers were log transformed for ANOVA.

Primary Nutrition of Phloem. our phloem discs (125 mm²) were collected from each tree during resin sampling on site 1. Two disks per tree were lyophilized, ground, and analyzed for total N with a Carlo-Erba model Na 1500 N (Carlo-Erba, Milan, Italy). To ensure quality control, every tenth sample was apple leaf tissue of known nitrogen content (National Institute of Standards and Technology, U.S. Department of Commerce). Two other disks per tree were dried and weighed to provide a gravimetric estimate of phloem thickness.

We compared the suitability of each species' phloem for *O. minus*, using fifteen bolts cut on 8 August 1999 from three trees of each species (5, 43-cm long bolts/tree). On 11–12 August 1999, each bolt was inoculated in two horizontal rows of alternating *O. minus* and blank control treatments at eight equidistant sites around the bolt. On days 7, 16, 23, and 28 after inoculation, the bark from two treatment and two control inoculations per bolt were removed and the area colonized by *O. minus* was measured. Because resin flow and lesion formation is greatly reduced in cut bolts compared with standing trees, any differences between pine species in fungal growth would

have been likely a result of primary nutritional quality of the phloem rather than secondary metabolism. The data were square-root transformed and analyzed with an ANOVA model that included species as a fixed effect and tree nested in species as a random effect.

Simulation Model. We developed a simulation model to evaluate the composite reproductive success of hypothetical *D. frontalis* infestations within stands that contained different mixtures of Virginia pine and loblolly pine. In each simulation, one cohort of recently eclosed reproductive adults attacked, reproduced, and reemerged or died within the trees. Surviving adults attacked subsequent trees and initiated additional broods of offspring until none of the initial cohort remained. The model was defined by three equations:

$$Ro = \sum_{b=1}^{\infty} \sum_{t=1}^{40} (Enter_{t,b} \cdot R_{t,b}), \quad [1]$$

where $Enter_{t,b}$ = proportion of beetles that enter tree t to initiate brood b (this incorporates beetle attack preferences for individual trees and survival from one brood to the next); and $R_{t,b}$ = per capita reproduction (adult offspring/adult) of beetles producing brood b that enter tree t . Thus, Ro represents the per capita reproduction per lifetime for a cohort of adult beetles that participate in sequential attacks until all in the initial cohort have died. We chose 40 as the number of host trees for each brood because this was approximately the number of trees we measured and approximates the number of trees under attack at one time in a medium-sized infestation.

$$\sum_{t=1}^{40} Enter_{t,1} = 1 \quad \text{and} \quad [2]$$

$$\sum_{t=1}^{40} Enter_{t,b+1} = \sum_{t=1}^{40} (Enter_{t,b} \cdot Reemerge_{t,b} \cdot Sbetween), \quad [3]$$

where, $\sum_{t=1}^{40} Enter_{t,b}$ = proportion of the original cohort surviving to produce brood $(b + 1)$ in the next set of attacked trees, which equals the sum of the products of the proportion of beetles that entered each tree for brood (b) , the tree-specific probability of surviving to reemerge ($Reemerge_{t,b}$), and the probability of surviving to enter the phloem of the next tree ($Sbetween$). $Sbetween$ is regarded as a function of predation on the bark surface (especially by *T. dubius*) and was treated as a constant value for all trees in the forest. Different simulations were run with high and low values of $Sbetween$. ($Sbetween = 0.80$ and 0.43 , respectively; Pope et al. 1980).

The simulated composition of the forest was varied from 40 Virginia pine:0 loblolly pine to 39:1, 38:2,..., 0:40. Values for $R_{t,b}$, $Enter_{t,b}$, and $Reemerge_{t,b}$ were randomly assigned to each tree, for each brood,

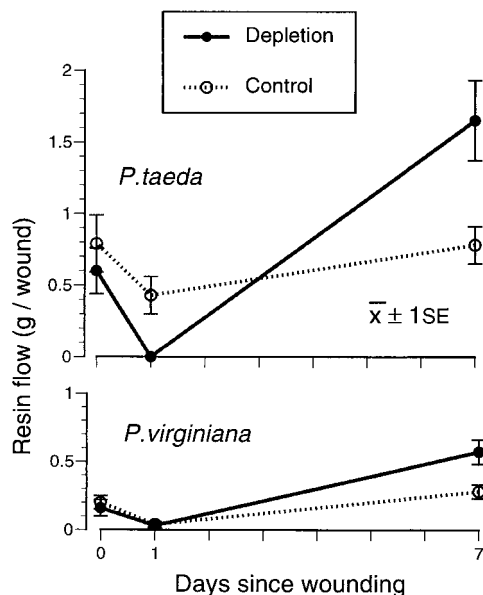


Fig. 1. Resin flow in loblolly pine and Virginia pine before and after resin depletion treatments (applied to one side of each tree just after measurements on days 0 and 1).

depending on its species designation, from frequency distributions that matched empirical data from this study. $R_{t,b}$, $Enter_{t,b}$, and $Reemerge_{t,b}$ were assumed to be uncorrelated among trees within species (as indicated by our data). Twenty replicate simulations were run for each possible species composition, which was enough so that additional simulations had little effect on average R_o . For calculations, maximum b was set at 15, but with our estimated values of $Reemerge_{t,b}$ and $S_{between}$, the median beetle produced no more than 4 broods (entered no more than 4 trees), so there were seldom appreciable contributions to lifetime reproduction beyond brood 5.

We ran one set of simulations under a scenario of attack preferences for Virginia pine (as indicated by our data from site 2), and another under a scenario of no discrimination (as indicated by data from site 3). In the former, $Enter_{t,b}$ averaged twice as high for Virginia pine as for loblolly pine, whereas in the latter it averaged the same for both species. Each of these scenarios was evaluated for conditions of high and low survival between attacks.

This model was not intended as an operational tool to predict beetle population growth. This would require validation with independent data. Instead it was developed to understand the demographic consequences for beetles of observed patterns in host preference and host-specific reproductive performance. It also had heuristic value in being the first mathematically explicit model that we know of for projecting beetle population dynamics as a function of the mixture of host species.

Results

Resin Defenses in Experimentally Wounded Trees.

Constitutive resin flow of Virginia pine was much lower (approximately one-half) than that of loblolly pine (Fig. 1; $F_{1,28} = 11.99$, $P = 0.002$). In both species, resin flow dropped to near 0 on day 1 following the depletion treatment, but increased to about twice the baseline levels by day 7 following depletion (Fig. 1; $F_{2,142} = 135.99$, $P < 0.0001$, for effect of day). Species \times day, species \times treatment, and day \times treatment interactions were all significant ($F_{2,142} = 4.54$, $P = 0.012$; $F_{1,142} = 4.96$, $P = 0.028$; and $F_{2,142} = 30.00$, $P < 0.0001$, respectively).

In another set of trees (site 4), resin flow was again much higher in loblolly pine than Virginia pine: mean \pm SE after 3 h = 2.20 ± 0.36 versus 0.66 ± 0.27 g/wound ($n = 10$ and 12 trees, respectively). Additional resin flow during the time from 3 to 24 h after wounding was similar and still much higher in loblolly pine: 2.39 ± 0.38 versus 0.66 ± 0.16 g/wound. During the time from 24 to 72 h, additional resin flow declined more sharply in loblolly pine than in Virginia pine: 0.94 ± 0.22 versus 0.48 ± 0.20 g/wound.

Attack Preferences and Resin Flow During Attack.

In a third set of study trees (site 2), before natural attack, constitutive resin flow of Virginia pine was also much lower than that of loblolly pine (Table 1). When the advancing infestation reached our study site, the baited sample trees of both species came under attack at the same time (mean attack initiation \pm SE = 3 August \pm 0.33 versus 4 August \pm 0.23 d for Virginia versus loblolly pine). However, subsequent to the initiation of attacks, beetles landed on Virginia pine 1.6 times more frequently than on loblolly pine (Table 1). *T. dubius* landing rates did not differ between the tree species. Based on pitch tube counts, *D. frontalis* attacked Virginia pine 2.1 times more densely than

Table 1. Comparisons of *P. virginiana* vs. *P. taeda*, before and during attacks by *D. frontalis*, within a mixed species pine stand (site 2) in the Bankhead National Forest, Alabama. Study trees were under attack from 28 July–26 August 1999

Parameter	<i>Pinus virginiana</i> mean \pm SE	<i>Pinus taeda</i> mean \pm SE	Species comparison
Resin flow before attack (g/wound)	0.22 \pm 0.09	1.71 \pm 0.25	$F_{1,28} = 48.62^{***}$
<i>D. frontalis</i> landings/450 cm ²	114 \pm 13	73 \pm 11	$t_{28} = 2.40^*$
<i>D. frontalis</i> attacks/m ²	128 \pm 22	62 \pm 11	$t_{28} = 3.71^{***}$
Attacks/landing	0.061 \pm 0.016	0.044 \pm 0.011	$t_{28} = 1.22$
<i>T. dubius</i> landings/250 cm ²	46.3 \pm 4.5	40.0 \pm 4.5	$t_{28} = 0.97$
Δ resin flow during attack (g/d)	-0.008 \pm 0.007	-0.005 \pm 0.007	$t_{28} = 0.33$

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

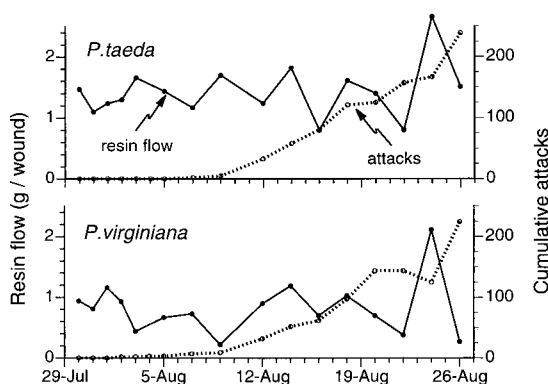


Fig. 2. Representative patterns of oleoresin flow during the course of beetle attacks on one individual each of loblolly pine and Virginia pine. Figure 3 summarizes these patterns for all study trees.

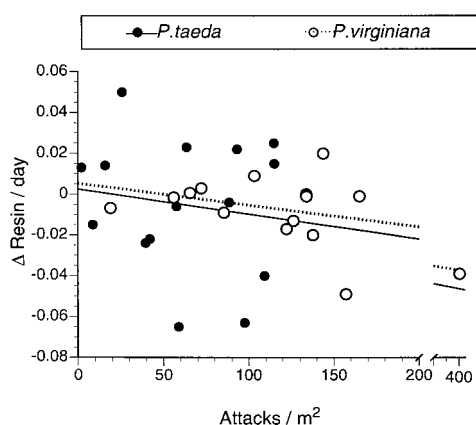


Fig. 3. The daily change in resin flow, from days 0–30 of beetle attack, as a function of attack density on day 30 for loblolly pine and Virginia pine. Regressions did not differ between species ($P > 0.20$).

loblolly pine. Attacks per landing by *D. frontalis* were $\approx 5/100$ for both tree species (Table 1).

After the initiation of attack, resin flow in both species remained relatively constant (Figs. 2 and 3). The slope of resin versus day was significantly different from 0 for only three trees of each species. The average Δ resin/d was only slightly negative and indistinguishable between species (Table 2). Beetle attack density also had no detectable effects on Δ resin/d (Fig. 3; $F_{1,26} = 1.32$, $P = 0.26$). Nor was Δ resin/d affected by interactions between species and attack density ($F_{1,26} = 0.01$, $P = 0.94$).

Over the entire 1-ha plot (site 2), every tree that was attacked by *D. frontalis* died, although there was a strong disparity between pine species in the probability of being attacked. Nearly every Virginia pine was attacked, whereas 37% of loblolly pine escaped attack (attacks = 56 of 57 versus 30 of 48; $G = 25.7$, $df = 1$, $P < 0.0001$). All trees that escaped attack were still alive 1 yr later.

Colonization Success of *D. frontalis*, *O. minus*, and *Tarsonemus* spp. In site 3, where pine species were segregated toward different corners of the plot, attack densities were similar between pine species (Table 2); this differed from the results for site 2 (Table 1).

Reemergence of attacking *D. frontalis* adults was only 56% in Virginia pine compared with 90% in loblolly pine (Table 2). Of the adults that did not reemerge, all were dead and most were encrusted in resin within the phloem. Total length of oviposition galleries per 250 cm^2 was somewhat higher, but insignificantly so, in loblolly pine (Table 2). However, the number of eclosed larvae per area or per dm of oviposition gallery was about twice as high in loblolly pine as in Virginia pine (Table 2). Furthermore, larval survival was more than twice as high in loblolly pine as in Virginia pine (Table 2). By virtue of increased oviposition and increased larval survival, average per capita reproductive success of *D. frontalis* was approximately fivefold higher in loblolly pine than in Virginia pine: mean \pm SE = 4.65 ± 1.40 versus 0.89 ± 0.33 pupae/attack (Table 2). Neither percent of area colonized by *O. minus*, nor density of *Tarsonemus* mites differed between tree species (Table 2).

Oleoresin of loblolly pine appeared to have stronger antifungal properties than the oleoresin of Virginia pine; i.e., live adults excavated from fresh, resinous, attack sites in loblolly pine carried fewer viable fungal propagules on their exoskeletons than similar beetles

Table 2. Colonization of *P. virginiana* vs. *P. taeda* on site 3 by *D. frontalis*, *O. minus*, and *Tarsonemus* spp. Replicate bark samples were removed from 8–10 trees of each species during beetle pupation

Parameter	<i>Pinus virginiana</i>		<i>Pinus taeda</i>		Species comparison
	mean \pm SE	SD ^a	mean \pm SE	SD ^a	
Attacks (<i>D. frontalis</i> entries/250 cm^2)	5.85 \pm 0.80	1.93	5.28 \pm 1.20	1.10	$F_{1,16} = 0.17$
Proportion of adults re-emerging	0.56 \pm 0.09	0.22	0.90 \pm 0.06	0.16	$F_{1,16} = 8.97^{**}$
Oviposition gallery (cm/250 cm^2)	55.3 \pm 9.8	38.8	74.8 \pm 8.5	17.5	$F_{1,16} = 2.66$
Hatched larvae/250 cm^2	16.9 \pm 5.5	24	34.5 \pm 5	10.8	$F_{1,16} = 7.53^{**}$
Hatched larvae/dm of oviposition gallery	2.55 \pm 0.64	2.66	4.64 \pm 0.58	1.65	$F_{1,16} = 6.49^{**}$
Larval survival (%)	29 \pm 9	23	67 \pm 6	22	$F_{1,16} = 10.40^{**}$
Pupating larvae per attack	0.89 \pm 0.33	0.35	4.65 \pm 1.40	4.36	$F_{1,16} = 6.49^{**}$
Prevalence of <i>O. minus</i> (% bluestain)	38 \pm 7	27	55 \pm 6	14	$F_{1,16} = 3.20$
Abundance of <i>Tarsonemus</i> spp. (250 cm^{-2})	855 \pm 705	1663	378 \pm 175	318	$F_{1,16} = 0.92$

^a Estimated standard deviation among trees from nested ANOVA. Variance among trees within species was significant at $P < 0.05$ for all.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

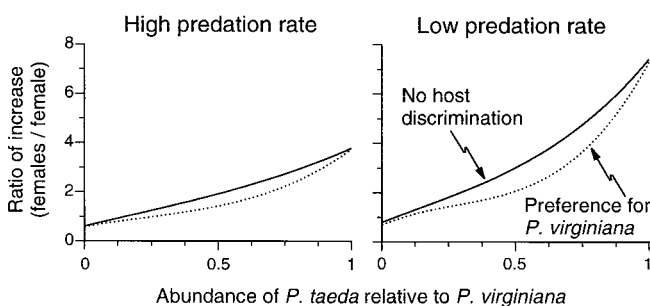


Fig. 4. Results from simulation models testing the effect of changes in host species composition, host discrimination, and predation intensity on average reproductive success of *D. frontalis* (offspring \cdot adult $^{-1}$ generation $^{-1}$; R_o , equation 1). Simulated forests were comprised of trees that matched our empirical frequency distributions for pupae/attack and percent reemergence. Under the scenario of no host discrimination, *D. frontalis* attack rates were equal for both species. Under the scenario of host discrimination, *D. frontalis* attacked Virginia pine at twice the density of loblolly pine (as in Table 1). The probability of a reemerging adult surviving to enter the phloem of another tree was set at 0.43 (high predation) or 0.80 (low predation).

excavated at the same time from Virginia pine within the same stand (mean \pm SE = 0.17 ± 0.12 versus 3.0 ± 1.1 colonies/beetle; $F_{1,15} = 6.81$, $P = 0.019$). Adult beetles captured at the same place and time in funnel traps, which had not been interacting with oleoresin, carried much higher loads of fungi on their exoskeletons (mean \pm SE = 51.9 ± 21.7 colonies/beetle).

Primary Nutrition of Phloem. Nitrogen content of phloem in healthy unattacked trees was slightly, but significantly, lower in Virginia pine than in loblolly pine: mean \pm SE = 0.25 ± 0.01 versus $0.28 \pm 0.01\%$ dry mass ($F_{1,25} = 8.71$, $P = 0.007$). Phloem thickness, as measured by area-specific mass was very similar between species: mean \pm SE = 55 ± 3 versus 59 ± 3 mg/125 mm 2 for Virginia pine and loblolly pine, respectively ($F_{1,28} = 0.06$, $P = 0.80$). After 2 wk of growth in freshly cut bolts from unattacked trees, the area colonized by inoculations of *O. minus* was threefold greater in loblolly pine compared with Virginia pine: mean \pm SE = 50 ± 14 versus 15 ± 3 cm 2 /inoculation ($F_{1,4} = 5.95$, $P = 0.07$).

Simulation Model. A simulation model predicted that varying the species composition of Virginia pine versus loblolly pine would strongly affect the population growth of *D. frontalis* (Fig. 4). The expected ratio of population increase per generation (R_o) increased from <1 in a hypothetical forest with all Virginia pine to 4–8 (depending on predation rate) in a forest with all loblolly pine (Fig. 4). When simulated *D. frontalis* did not discriminate between tree species, R_o increased approximately linearly from 100% Virginia pine to 100% loblolly pine. However, when *D. frontalis* preferentially attacked Virginia pine, R_o increased as an accelerating function as forest composition changed from 100% Virginia pine to 100% loblolly pine. High predation led to decreased R_o and less-pronounced effects of host preference as compared with low predation. R_o varied less among replicate simulations when Virginia pine dominated the forest, than when loblolly pine was the more common species. The proportion of the initial adult cohort reemerging to colonize successive trees did not differ

between host discrimination scenarios, but declined with increasing abundance of Virginia pine, and decreased precipitously with increased predation. Given low predation, 55% of the cohort survived to colonize a second tree, as compared with only 29% under the scenario of high predation.

Discussion

Host Preferences. When pine species were intermixed, *D. frontalis* tended to land on, and attack, Virginia pine more frequently than loblolly pine (Table 1). A survey after the infestation further indicated that Virginia pine were less likely to escape attacks than loblolly pine. Some other bark beetle species also discriminate among host species (Tunsted et al. 1993, Lieutier et al. 1997, Brattli et al. 1998, Siegert and McCullough 2001). Host selection may occur before landing, via vision or olfaction, or after landing, via contact chemoreception (Bunt et al. 1980, Wood 1982, Payne 1986, Byers 1995). In our study, the probability that a beetle would attack once it had landed was similar for both pine species, which, together with the differences in landing rates, indicates that *D. frontalis* host selection occurred in flight (at least during the aggregation phase of attacks). This differs from some other bark beetle systems in which host selection seems to be primarily a function of contact chemoreception after a beetle has landed (Elkinton and Wood 1980, Hynum and Berryman 1980, Moeck et al. 1981, Raffa and Berryman 1982, Wallin and Raffa 2000). Differences in landing rates between species (Table 1) were probably attributable to differences in secondary attraction (*sensu* Payne 1980). α -Pinene, which synergizes the attraction of frontalin to flying beetles (Payne et al. 1978), comprises $>95\%$ of the monoterpenes in the oleoresin of Virginia pine, compared with $\approx 55\%$ in loblolly pine (Mirov 1961, Hodges et al. 1979). Thus, Virginia pine that are attacked by pioneer beetles probably develop more attractive plumes of volatiles, which contribute to rapid aggregation by additional beetles. There are several other

potential mechanisms by which pine species could differ in their secondary attraction (Fäldt 2000, Seybold et al. 2000, Miller and Borden 2000).

The observed differences in landing rates (Table 1) do not require any difference between species in primary attraction. However, the post-infestation survey showed that Virginia pine were much less likely than loblolly pine to escape attack, which implies that Virginia pine were more likely to be initially colonized (none of the 19 surviving trees in site 2, 18 of them loblolly pine, had pitch tubes or showed any other signs of beetle attack). *D. frontalis* could potentially distinguish among previously uncolonized hosts via chemoreception and/or vision (Payne 1975, Gollob 1980, Strom et al. 1999). Pine species can differ in the release rates and chemical composition of volatiles (especially monoterpenes; Mirov 1961, Hodges et al. 1979), which can influence primary attraction of some bark beetles (Volz 1988, Tunset et al. 1993, Huber et al. 2000). There is accumulating evidence that vision in general, and color in particular, influences the orientation behavior of bark beetles in general and *D. frontalis* in particular (Jenkins 1983, Strom and Goyer 2001, Strom et al. 2001). To our eyes, the most conspicuous visual differences between Virginia pine and loblolly pine are bark color, branching patterns, and silhouette, but it is challenging to deduce the visual cues employed by other species (Groberman and Borden 1982, Endler 1993). Whatever their proximate cause, the differences in preference were large enough so that mortality from beetles, in one year, altered the species composition of pines in a one ha study area from 57:48 (Virginia pine:loblolly pine) to 1:18. If this pattern is general, *D. frontalis* must exert a significant influence on the composition of *Pinus* communities.

D. frontalis did not always display preference for Virginia pine versus loblolly pine. In site 3, where the pine species were largely segregated into different halves of a 1-ha area, final attack densities were no different between species (Table 2). We hypothesize that these sites differed because beetles choose among trees at a relatively fine spatial scale (Byers 1993, 1999), but it might also be attributable to season (the segregated site was attacked 6–8 wk earlier than the intermixed site), or chance variation in the local abundance of flying beetles (Borden et al. 1986). There would be value in comparing beetle attack preferences for these two species across replicate stands drawn from a broader forest landscape than was studied here.

Host Suitability. Despite their tendency to prefer Virginia pine, *D. frontalis* had very poor reproductive success in Virginia pine (Table 2; Fig. 4). *A priori*, we hypothesized that differences in host suitability could be attributable to (1) resin defenses, or (2) nutritional quality of phloem for beetle larvae or their fungal associates.

Resin flow tends to be negatively related to host suitability for *D. frontalis* because it can interfere with gallery excavation and oviposition, or even entomb and kill adults (Hodges et al. 1979, Reeve et al. 1995).

Indeed, the proximate causes for reduced reproduction in Virginia pine included all of these factors (Table 2). However, our measurements of resin flow do not permit a simple explanation. In three different comparisons, Virginia pine had markedly lower constitutive resin flow than loblolly pine (Fig. 1; Table 1, text). Furthermore, there was no evidence from experimental resin depletion or resin dynamics during natural attacks that Virginia pine can synthesize new oleoresin more rapidly than loblolly pine (Fig. 1; Table 1). The disparity in reproductive success between host species might be a result of interspecific variation in the chemical and physical properties of resin that influence its toxicity and efficacy in impeding and trapping beetles. For example, resin viscosity, crystallization rate, and limonene content differ among some other host species of *D. frontalis* (*P. taeda*, *P. palustris*, *P. echinata*, and *P. elliottii*; Coyne and Lott 1976; Hodges et al. 1977, 1979). The abundance of numerous large pitch tubes on the boles of attacked Virginia pine, and extensive resinosis within the phloem, suggested that the effects on *D. frontalis* of Virginia pine resin were greater than implied by our standardized measurements of resin flow. One possibility is that the oleoresin of Virginia pine flows from wounds for a longer time by virtue of slower crystallization or different anatomy of the resin duct system. This hypothesis received some support in that resin flow declined less from 24 to 72 h after wounding in Virginia pine versus loblolly pine, but the support was equivocal in that resin flow from Virginia pine was still no greater than that from loblolly pine. More studies are needed to evaluate the roles of resin viscosity and crystallization rates in host suitability for *D. frontalis*.

The proximate explanation for low reproductive success in Virginia pine versus loblolly pine also included low larval survival (Table 2). This could have been because of reduced nutritional value of phloem for beetle larvae or for their mutualistic fungi. In fact, nitrogen content was slightly lower in Virginia pine, but the difference was so small (0.25 versus 0.28% dry mass) that it seems unlikely to explain patterns in larval survival (Ayres et al. 2000). Phloem thickness, which can also affect larval survival of bark beetles (Haack et al. 1984), was almost identical between species. Other aspects of phloem chemistry, e.g., water content, nonstructural carbohydrates, or terpenes, could still differ between pine species in ways that matter to beetle larvae or their fungal associates. In fact, the growth of *O. minus* (a bluestain fungus) was approximately threefold greater in loblolly pine than in Virginia pine. More study is required to judge whether phloem from loblolly pine supports better growth of the mutualistic fungi *Entomocorticium* sp. A and *C. ranaculosus*. Increased growth of *O. minus*, unless it is outweighed by increased growth of mutualists, would actually be an impediment to larval success (Lombardero et al. 2003). Results contradicted the hypotheses that host suitability was inversely related to prevalence of bluestain or *Tarsonemus* mites (Table 2), or was because of differential antibiotic activity of oleoresin on nonbeneficial fungi carried on

beetle exoskeletons. A possible explanation for low larval survival in Virginia pine is that growth of mycangial fungi was inhibited by the secondary metabolites that impregnated the phloem of Virginia pine during attacks (Bridges 1987).

Low survival in Virginia pine could also be a result of increased parasitism. The density of eight species of parasitoids (Braconidae, Eurytomidae, and Pteromalidae) all tend to increase with decreasing bark thickness (Gargiullo and Berisford 1981), and bark thickness is conspicuously less in Virginia pine than in loblolly pine.

Causes and Consequences of Nonadaptive Host Preferences. Regardless of the mechanistic causes for poor reproduction in Virginia pine, it remains paradoxical why *D. frontalis* displays a behavioral preference for the worst of two native host species. The simplest explanation invokes the higher content of α -pinene in Virginia pine. α -Pinene is a ubiquitous component of the oleoresin in *Pinus*, and is released as a volatile when trees come under attack. Natural selection has presumably favored the incorporation of this signal into the host location behavior of *D. frontalis* (Byers 1995). The apparent preference of *D. frontalis* for Virginia pine may be an artifact of this host orientation system (stronger attraction to trees emitting more α -pinene) rather than a result of selection for preferential use of Virginia pine over loblolly pine. Another consideration is that the relative abundance of host species has changed dramatically in recent evolutionary time. It is only since the 20th century that loblolly pine has come to form extensive monospecific stands such as now dominate the southeastern United States (Wahlenberg 1960). In contrast, Virginia pine was apparently more common than it is today in approximately one-half of the precolonization forests that harbored *D. frontalis* (Critchfield and Little 1966, White and Lloyd 1998). Thus, *D. frontalis* may have a stronger search image for Virginia pine by virtue of having more history of evolutionary interactions with it than with loblolly pine (Newby and Etges 1998, Singer et al. 1993).

Current techniques used to control *D. frontalis* outbreaks are frequently insufficient to suppress regional outbreaks and tend to be destructive in that they involve cutting down infested trees plus a buffer strip of uninfested trees (Cronin et al. 1999). An alternative, long-term approach would be to manage forests for pine species that limit *D. frontalis* reproductive success (Belanger et al. 1993). Increasing the relative abundance of *Pinus* species that are of low quality for *D. frontalis* (e.g., Virginia pine) could limit population growth and therefore the extent of infestations. Implementation of such management practices would require careful consideration of factors that differ among pine species such as ease of regeneration, growth rate, timber value, recreation quality, and consequences for biodiversity. Increasing the abundance Virginia pine would have costs to forest industry because Virginia pine generally grows more slowly and has lower timber value than loblolly pine. However, these costs could be compensated by reduced losses to

beetle outbreaks. Our simulation models provide a starting point for assessing the demographic effects on *D. frontalis* of different mixes of Virginia pine and loblolly pine. The preference of *D. frontalis* for the less suitable host has a favorable consequence in that a relatively low percentage of Virginia pine can produce a disproportionately large reduction in beetle population growth. Our simulations indicate that beetle population growth is about halved in forests that contain 25% Virginia pine compared with forests that lack Virginia pine (Fig. 4). In this sense, a host species such as Virginia pine can function like a trap crop that is used to control losses and protect neighboring crops from agricultural pests (Hokkanen 1991). Similar explanations may hold for the pattern of reduced pest damage in willow plantations that are mixed varieties versus monocultures (Peacock et al. 2001).

Additional research would be appropriate before deploying Virginia pine on a broad scale to mitigate beetle impacts. One mechanism that could produce an opposing pattern is if endemic populations are more easily sustained in forests that contain Virginia pine because the beetles are able to aggregate more effectively on these hosts. Also, the effects of host species composition on forest epidemiology probably depends upon the spatial scale at which tree species are mixed. For example, Virginia pine seems more susceptible to beetles than loblolly pine when trees are intermixed on a scale of meters, but beetle infestations within stands of Virginia pine should be less likely to grow than infestations within stands of loblolly pine (Fig. 4). Thus, compared with loblolly pine, stands of Virginia pine may be less susceptible to beetles even while individual trees within mixed stands are more susceptible. The interaction of host species composition and predators (Fig. 4), which influence the endogenous population cycles characteristic of *D. frontalis* (Turchin et al. 1999), creates the potential for additional, more complex effects on the period, amplitude, and acceleration of *D. frontalis* outbreaks and declines in forests that differ in their host species composition.

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